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Within-species variation eclipses between-species differences in *Pan* consolation

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ABSTRACT

Empathy and its subcomponents are well documented throughout the animal kingdom, indicating the deep evolutionary origins of this socioemotional capacity. A key behavioural marker of empathy is consolation, or unsolicited bystander affiliation directed towards distressed others. Consolation has been observed in our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*). However, systematic comparisons are absent, despite potential for interspecific differences. Bonobos are often considered less aggressive, more emotionally sensitive, and more socially tolerant than chimpanzees—key characteristics purported to drive consolation. Furthermore, social and individual factors also appear to drive intraspecific variation in empathy. To address within- and between-species variability in *Pan* consolation, we systematically tested the consolatory tendencies of $N = 40$ bonobos and $N = 50$ chimpanzees. Bonobos and chimpanzees exhibited similar consolation tendencies; however, within-species analyses revealed further similarities and variation. Bonobo consolation was most often directed towards and received by younger individuals, while chimpanzee consolation was most often directed towards close social partners. In addition, males and females of both species showed decreased consolation with age, with some evidence for chimpanzee males consoling more than young females. Our findings support the notion that within-species variation in *Pan* socio-emotional abilities is greater than between-species differences, highlighting the presence of striking behavioural diversity across our two closest cousins.

1. Introduction

Empathy, broadly defined as sharing and/or understanding others' emotional states, is a cornerstone of the human experience (Eisenberg & Strayer, 1990; Preston & de Waal, 2002). From politics and marketing to day-to-day social interactions, empathy allows us to effectively cooperate and communicate as well as strengthen our social relationships (de Waal, 2007). Cross-cultural and personality studies have revealed remarkable individual and cultural variation in empathic concern and perspective-taking (Chopik et al., 2017;Eisenberg et al., 1995, 1999; Knafo et al., 2008). Some longitudinal studies indicate that individual differences in human empathic responding are relatively stable (Eisenberg et al., 1995, 1999; Knafo et al., 2008). As variation has been reported on individual and cultural levels, it has been suggested that both personality and cultural norms may influence empathy. Likewise, it is often suggested that humans exhibit a uniquely advanced capacity for empathy, related to our advanced socio-cognitive capacities including perspective taking, self-other differentiation, emotion regulation and cognitive appraisal (Decety et al., 2012). However, social neuroscience and comparative research suggest that empathy emerges from foundational bottom-up processes, such as emotion sharing, with deep evolutionary roots (Adriaense et al., 2020; de Waal & Preston, 2017), which is appraised and understood through top-down regulatory mechanisms (i.e., cognitive processing (Decety & Lamm, 2006).

In the animal kingdom, many behaviours possibly related to empathy have been reported, mainly in mammals (Adriaense et al., 2020; Pérez-Manrique & Gomila, 2018) though there is also some evidence in birds (e.g., consolation in *Corvus corax*; Fraser & Bugnyar, 2010). Empathy-driven behaviours emerge in the form of subcomponents that represent differing expressions of emotional

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responsiveness and understanding (Brooker et al., 2022; de Waal, 2007). Some of these sub-components, such as emotional contagion, have been observed across many social mammals, indicating a deep evolutionary history (Adriaense et al., 2020). Furthermore, some behavioural prosocial manifestations of empathy, such as consoling others in distress, have been observed in rodents (Burkett et al., 2016), elephants (Plotnik & de Waal, 2014), and some primates (for a review, see Brooker et al., 2022).

Consolation, sometimes referred to as 'sympathetic concern' (Batson et al., 1987), is thought to require both a cognitive appreciation (and even understanding) of another's state combined with a prosocial orientation to improve it, such as by providing reassuring contact (de Waal, 2008). Among non-human animals, our two closest relatives, the bonobos and chimpanzees are shown to engage in consolation in a range of settings, including captivity, sanctuaries, and even the wild (Brooker et al., 2024; Clay & de Waal, 2013a; Palagi et al., 2004; Romero et al., 2010; Wittig & Boesch, 2003). Among wild chimpanzees, both the western and eastern subspecies have been observed to console others, including at Taï National Park, Ivory Coast (Wittig & Boesch, 2003) and the Mahale Mountains National Park, Tanzania (Kutsukake & Castles, 2004) respectively.

Another study of the eastern subspecies in Budongo Forest, Uganda, showed that consolation only occurred after 3.3 % of observed conflicts, which was not significantly more than matched controls (Arnold & Whiten, 2001). In contrast, Kutsukake and Castles (2004) observed consolation after around 22 % of conflicts in the Mahale M-group of eastern chimpanzees. This difference between the Mahale and Budongo groups indicate possible within-species behavioural flexibility and cross-community variation in consolatory tendencies. Whilst there are no studies of consolation in wild bonobos, case studies of targeted prosocial behaviour, such as conspecifics attempting to remove snares from group members and searching for lost group members (Tokuyama et al., 2012) suggest consolation is likely. Moreover, consolation has been observed in sanctuary-settings (Clay & de Waal, 2013a), including by wild-born immature individuals, suggesting that consolation is likely part of the wild bonobo repertoire.

Evidence that immature apes engage in consolation challenges assumptions that consolation is dependent on sophisticated cognitive mechanisms. In both bonobos and chimpanzees, younger individuals are most likely to offer consolation (Clay & de Waal, 2013a; Webb et al., 2017), indicating that empathic orientation towards other's states may be more intrinsic than previously thought. In humans, concern for others including consolation has been reported even within the first year of life, as early as nine months (Davidov et al., 2021). Empathic behaviours, like consolation, may strengthen interpersonal bonds, especially for dyads that demonstrate enduring cooperative relationships. For this reason, social closeness, familiarity, or similarity has been shown to be a key predictor of empathic tendencies in humans (Lindegaard et al., 2017; Norscia & Palagi, 2011) and among nonhuman apes (bonobos: Clay & de Waal, 2013a; Palagi & Norscia, 2013; chimpanzees: Fraser et al., 2008; Romero et al., 2010; Webb et al., 2017).

Bonobos and chimpanzees develop long term enduring bonds with other group members and form strong support networks (Gruber & Clay, 2016); yet there are reported differences in their social tendencies and socio-emotional orientations. For example, bonobos appear to have enhanced attentiveness to conspecific social and emotional expressions than chimpanzees (F. Kano et al., 2015; Kret et al., 2016) and some experimental paradigms have indicated that bonobos outperform chimpanzees on cooperation (Hare et al., 2007) and theory-of-mind-related tasks (Herrmann et al., 2010). Furthermore, chimpanzees tend to be xenophobic to other communities (Wilson & Wrangham, 2003). In contrast, wild bonobo communities can be vocally hostile to other groups and yet numerous populations regularly have peaceful intergroup encounters, even cases of food sharing and exchanges of sex, grooming, and play (Furuichi, 2011; Lucchesi et al., 2020). Finally, whilst there are recent indications of an overlap in male aggressivity (Mouginot et al., 2024), lethal aggression is only confirmed thus far for chimpanzees, albeit rare and variable between communities (Wilson et al., 2014).

Apparent socio-emotional variation between the *Pan* apes has been suggested to have biological and neurological foundations. Firstly, chimpanzees, but not bonobos, have been shown to have deletion of the DupB region in the AVPR1A gene, which includes a microsatellite called RS3 (Staes et al., 2014). Variation in RS3 is linked with variation in social bonding, and increased levels in bonobos may support their reported xenophilia. Neurological research further shows that bonobos have twice the density of serotonergic axons in the amygdala than chimpanzees (Stimpson et al., 2016), a region associated with social cognition and emotional regulation. These neurobiological differences have been purported to mediate the observed differences in their social structures and behaviour. For example, the ability to regulate one's emotions—suppressing personal arousal in response to an arousing situation—is a crucial precursor to empathy (Eisenberg et al., 1994; Lockwood et al., 2014). Bonobos also have more grey matter in the right dorsal amygdala and right anterior insula than chimpanzees, along with a larger pathway linking the amygdala with the ventral anterior cingulate cortex (Rilling et al., 2012). These regions are associated with perceiving distress in oneself and others, and to regulating reactive and proactive aggressive impulses. Such differences, coupled with purported increased perspective-taking and cooperation abilities may facilitate enhanced production of prosocial empathic behaviours, such as consolation and targeted helping, compared to chimpanzees.

Social tolerance is also posited to influence empathic tendencies, according to the *Social Constraints Hypothesis* (de Waal & Aureli, 1996). Evidence from other primate species supports this idea. For example, consolation has been observed in the socially tolerant Tonkean macaques (*Macaca tonkeana*; Palagi et al., 2014) and not in other more despotic macaque species (for a review, see Brooker et al., 2022). Whilst both *Pan* species are known to engage in consolation, they exhibit notable within-species variation in social tolerance (Cronin et al., 2014; Cronin et al., 2015; van Leeuwen et al., 2023). Furthermore, as previously mentioned, consolation appeared relatively absent in one population of eastern chimpanzees at Budongo (Arnold & Whiten, 2001) and yet present in their Mahale counterparts (Kutsukake & Castles, 2004). These communities have been demonstrated to vary considerably in social tolerance and hierarchical steepness, whereby Budongo chimpanzees have steeper, and more despotic hierarchies compared to Mahale (Kaburu & Newton-Fisher, 2015). Whilst these wild groups have not been systematically compared, these findings indicate that consolation may show intergroup variation and emerge flexibly if conditions permit. As population-level variation in group social tolerance can differ within species, consolatory tendencies may vary across groups living in similar conditions.

Whilst some socio-cognitive abilities of bonobos and chimpanzees have been compared, direct systematic comparisons of their consolation tendencies have yet to occur. Consolation does appear to be a feature of natural *Pan* social living; however, wild studies are scarce due to methodological constraints. Therefore, comparing great apes in semi-wild sanctuary settings can provide a balance of natural ecological surroundings with improved observational conditions. Based on evidence that bonobos show enhanced social awareness and emotional sensitivity (Herrmann et al., 2010; F. Kano et al., 2015; Kret et al., 2016), we tested the hypothesis that bonobos are more empathic than chimpanzees, predicting that bonobos would be more likely to console others than chimpanzees. Furthermore, following the hypothesis that empathy is socially-biased (Preston & de Waal, 2002), we predicted higher rates of consolation between dyads that are socially bonded, through kinship and close affiliative tendencies.

Consolatory tendencies tend to decrease in each species with age (Clay & de Waal, 2013a; Webb et al., 2017), whilst previous studies indicate a lack of general sex differences in consolation in bonobos and chimpanzees. However, as males remain in their natal groups in each species (Goodall, 1986; T. Kano, 1992), they might be expected to invest in building long-term social bonds already at a young age. In bonobos, males tend not to have strong social bonds beyond their mothers. They have been shown to form bonds with other females that extend their alliance relationships and improve reproductive success, however these are typically females with elevated rank positions, therefore reducing the likelihood that they would be victims of conflict (Surbeck et al., 2012, 2017). In chimpanzees, adult males are less likely to be victims of conflicts than females and immature males, implying that their closest social partners, other adult males, will have fewer opportunities to offer consolation. Furthermore, whilst no clear-cut age-related decline in comforting or prosocial behaviour is seen in humans (Pollerhoff et al., 2022), younger great apes may console more due to decreased tolerance and increased inhibition as individuals age. As such, and in line with previous findings (Clay & de Waal, 2013a; Webb et al., 2017), we predicted that, regardless of sex, younger individuals of both species will show the highest tendencies to console. In addition, we predicted an interaction between bystander age and sex in both species, whereby younger individuals of both sexes would show the highest consolatory tendencies whereas in adulthood, older males of each species would show lower rates than females. By comparing between- and within-species influences on an empathic behaviour like consolation in our closest living relatives, we aim to improve our understanding of the origins of human empathy and emotional responsiveness.

2. Methods

2.1. Subjects and housing

We conducted observations of bonobos at Lola ya Bonobo Sanctuary (hereafter, “Lola ya Bonobo”) in the Democratic Republic of the Congo during July–September 2019. We conducted observations of chimpanzees at Chimfunshi Wildlife Orphanage Trust (hereafter, “Chimfunshi”) in the Copperbelt Province of Zambia during March–August 2019. Lola ya Bonobo houses three groups of bonobos in enclosures ranging from 15 to 20 ha with rainforest, lake, swamp, stream, and open grass area, whilst Chimfunshi is home to four groups of chimpanzees that are accessible for observational research, living in outdoor miombo woodland enclosures ranging from 20 to 80 ha. At Lola ya Bonobo, bonobos sleep together in dormitories. At Chimfunshi, chimpanzees nest independently unless kept inside for monitoring or medical intervention.

Both sanctuaries house wild-born individuals, orphaned and rescued from the pet and bushmeat trades, as well as sanctuary-born individuals, all of whom are supported by caregiving and veterinary staff. In both sanctuary environments, the apes could roam, forage, and nest independently, whilst supported by an onsite caregiving team. The groups at Lola ya Bonobo sleep at night in a managed indoor dormitory and otherwise roam in their forested enclosures during the daytime. At both sites, groups are provisioned at least twice per day with a variety of fruits and vegetables.

At Lola ya Bonobo, we observed all inhabitants of Groups 1 and 2 (hereafter: B1 and B2), which housed $N = 22$ and $N = 18$ bonobos, respectively. At Chimfunshi we observed all inhabitants of Group 2 (hereafter: C2), the largest group which comprised $N = 50$ chimpanzees at the start of data collection. We logged 800 h of observations at Chimfunshi and 600 h of observations at Lola ya Bonobo. All data and code is provided as electronic supplementary material (hereafter: ESM). The age and sex composition of our sample is provided in Table S1 (see ESM).

2.2. Data collection

2.2.1. Victim focal follows

Consolation has typically been recorded using the post-conflict/matched-control method (de Waal & Yoshihara, 1983). This involves conducting focal follows of a victim for a standardised period—usually 5–10-min—after a conflict or spontaneous distress period, while recording the initiator and behaviour of all affiliative interactions that occur involving the focal victim. Post-conflict (PC) and post-distress (PD) periods are then compared with matched control (MC) recordings observed at a similar time and circumstance a day later. The PC/MC method has already reliably demonstrated consolation in multiple bonobo and chimpanzee communities compared with matched controls (Clay & de Waal, 2013a; de Waal & Aureli, 1996; Palagi et al., 2004; Romero et al., 2010), including in some of these sample populations (Clay & de Waal, 2013a). Thus, we decided to only collect post-conflict and post-distress events to ensure a large enough sample to compare individual and social influences on consolation tendencies.

We used focal all-occurrence sampling (Altmann, 1974) to collect $N = 150$ PCs and $N = 10$ PDs in C2. In B1, we observed $N = 28$ PCs and $N = 36$ PDs and in B2, we observed $N = 36$ PCs and $N = 16$ PDs. Our total sample of events was therefore $N = 276$ across both species and all three groups. Previous studies of consolation show that most consolatory interactions occur during the first minute after distress (Clay & de Waal, 2013a). We therefore conducted victim focals for the first 5-min following distress to optimise our limited observation time. We defined agonistic encounters by the presence of at least one of the following behaviours: high-contact aggression [hit, slap, kick, trample, bite], low-contact aggression [poke, push, push away, brush aside], chase, or threat [threat bark, swagger, display, flail arm, stamp] (Nishida et al., 2010). PCs were only analysed if the victim elicited a clear victim response, identified as the occurrence of bared-teeth scream, whimper, tantrum, or flee from aggression (Nishida et al., 2010) following an agonistic encounter. If these victim response behaviours occurred spontaneously, they were coded as PD events. During the 5-min focal-follows, we noted the presence of all bystanders within 1-m and 5-m of the focal subject at the onset of the event. We recorded all PC/PD victim focals using Panasonic HC-V770 Camcorders with detachable Sennheiser MKE 400 directional shotgun microphones.

2.2.2. Dyadic social affinity and gregariousness

We also collected focal scan follows (Altmann, 1974) of social tendencies to measure dyadic affiliation levels and individual gregariousness. We collected social focals outside of feeding times for both species. As we measured affiliation on a dyadic level, we accumulated information on individuals who were not currently the focal subject if they associated with the focal. The data set consisted of $N = 706$ focal follows for B1 (*range* = 28–41; $M = 32.1$; $SD = 11.0$), $N = 587$ focal follows for B2 (*range* = 16–44; $M = 34.2$; $SD = 11.3$), and $N = 684$ focal follows for the C2 (*range* = 9–18; $M = 14.3$; $SD = 2.6$). Each focal follow lasted 10-min and behaviours were recorded at 1-min scan points, upon which we recorded all social interactions the focal was involved in including grooming, play, and sex, as well as all individuals within 1-m. As the social behaviours required proximity of 1-m to the focal, we only coded either behaviour or proximity once per dyad per scan during observations. However, when we compared dyadic scores for behaviour and proximity when independent of one another, they were strongly correlated ($r(375) = 0.43$, $P < .001$). We thus incorporated all social behaviour observations into one score for proximity and used that to compute unique dyadic affiliation scores for every possible dyad. We divided the number of scan points each dyad interacted for by the total number of scan points both individuals of the dyad was observed for. We also computed individual gregariousness scores by dividing the total number of scans each focal subject was observed within proximity to at least one other individual by the total numbers of scans they were observed for. At Chimfunshi Wildlife Orphanage, we recorded social focal follows using the tablet app Zoo Monitor (Wark et al., 2019), which contributed towards long-term data collection of social relationships at this site. At Lola ya Bonobo, we recorded social focals by hand due to software incompatibility. In addition, we were interested in the effect of kinship and defined each dyad as ‘kin’ or ‘non-kin’ depending on whether they shared a maternal genetic relationship or not, respectively.

This therefore included all mother-infant, sibling-sibling, and grandparent-grandchild pairs as ‘kin’. Inter-observer reliability revealed almost perfect agreement between observers (partner identity: bonobo $\kappa > 0.80$; chimpanzee $\kappa > 0.96$; social behaviour: bonobo $\kappa > 0.95$; chimpanzee $\kappa > 0.93$).

2.2.3. Hierarchies

We assigned categorical rank values (high, medium, low) for each ape. For both species, we used the R package ‘EloRating’ (Neumann & Kulik, 2020) to create dominance scores based on dyadic agonistic interactions involving high-contact aggression, low-contact aggression, and chases (Neumann & Kulik, 2020). Each agonism type was assigned a different optimised weighting, known as a K-value, based on intensity and likelihood of winning probabilities. We only included individuals four-years and older with at least six observed dyadic agonistic interactions in this ELO analysis. For the chimpanzees, the ordered rank output was consistent with categorical rankings acquired from the keepers and care staff. Hence, we evenly divided this output into ‘high’, ‘medium’, and ‘low’ rank, and used the keeper allocations to assign categorical ranks to individuals for whom we lacked sufficient ELO data for. For the bonobos, the ELO analysis revealed ordered results that were broadly but not wholly consistent with keeper and researcher observations. Whilst human judgements of social rank may be influenced by observer bias, these slight inconsistencies were likely contributed to by a relatively lower quantity of agonistic observations over our relatively short study period, therefore affording our ELO analysis lower power. However, whilst the rank order was inconsistent, categorisation into ‘high’, ‘medium’, and ‘low’ was consistent with keeper and researcher observations. As we did not have substantial or prior quantitative data to support the ELO analysis, we decided to assign rank categories based on agreed deliberation between two long-term experienced observers of the bonobos at Lola ya Bonobo, supported by views of the sanctuary staff. For both species, we assigned mother ranks to infants (apes between 0 and 2 years of age). In both cases, observer rankings were based on observations of dynamics surrounding food and resource competition.

2.3. Ethics

This study was approved by the Senior Veterinary Advisory Team of Lola ya Bonobo Sanctuary, the Chimfunshi Research Advisory Board, and the Animal Welfare Ethics and Research Board of XXX University. Data collection comprised purely naturalistic observations and adhered to the legal requirements of the Democratic Republic of the Congo and Zambia, as well as the International Primatological Society’s Principles for the Ethical Treatment of Nonhuman Primates.

2.4. Data analyses

We conducted all-occurrence coding of affiliative and agonistic encounters during PC/PD periods in ELAN (ELAN, 2019; Wittenburg et al., 2006). Consolation was defined as the onset of an affiliative interaction involving contact during the 5-min follow that was spontaneously initiated by a bystander. Initiation was defined as the solicitation of an affiliative interaction either by gesturing or initiating physical contact with a partner. Thus, interactions initiated by the victim—e.g., the victim approached the bystander—were excluded as they do not represent spontaneous approaches by the bystander, thereby these interactions are not considered consolation (Das et al., 1998). Affiliative contact behaviours included body kiss, contact sit, embrace, finger/hand in mouth, embrace, genital inspection, genito-genital contact, grasp hand, groom, hunch-over, mount, mount walk, mouth kiss, pat, play, rump-rump touch, and touch (de Waal, 1988; Nishida et al., 2010; see Table S2). Inter-coder reliability of consolation occurrence and consoler identity indicated almost perfect agreement (consolation occurrence: bonobo $\kappa = 0.86$, chimpanzee $\kappa = 0.85$; consoler identity: bonobo $\kappa = 1.00$, chimpanzee $\kappa = 0.97$).

2.4.1. Summary of statistical approaches

We used a Bayesian mixed models approach to assess whether consolation was more likely to occur in the bonobo or chimpanzee groups sampled, along with within-species variation in consolation tendencies according to bystander and victim characteristics: sex, age, rank, gregariousness, and group, as well as the bystander-victim social relationship. We collapsed our observations into two formats: event-level, where each observation row represents one PC or PD event; and dyad-level, where each observation row represents a unique bystander-victim combination within an event. This allowed us to compare general species tendencies at the event-level and then to assess the influence of individual (e.g., bystander age, bystander sex) and social factors (e.g., kinship, affiliation score) on consolation at the dyad-level. We z-transformed all covariate predictors and dummy coded and centred all factor predictors prior to their inclusion as random slopes.

We fitted all models in RStudio (version 1.3.1093; RStudio Team, 2020) using the function brm of the package brms (version 2.21.0; Bürkner, 2017). Each model included four Markov chain Monte Carlo (MCMC) chains, with 10,000 iterations per chain, of which we specified 2000 iterations as warm-up to ensure sampling calibration. This resulted in 32,000 posterior samples in total for each model. In all models, we used default priors (weakly informative priors with a student’s t-distribution of 3 degrees of freedom and a scale parameter of 2.5) to ensure that our inferences were driven primarily by the data. Flat priors cover a wide range of parameter values without favouring any specific region. This allowed our already complex models incorporating many fixed and random effects to explore a broad parameter space, ensuring that no potential values are excluded a priori. Furthermore, flat priors emphasize the likelihood function, allowing the posterior distribution to closely follow the shape of the likelihood. Lastly, this approach also facilitates comparison with frequentist methods, enhancing the interpretability and generalisability of our findings.

For all models, we used multiple measures to summarise the posterior distributions for each variable and report evidence of an effect: 1) we characterised uncertainty by two-sided credible intervals (89 % CrI; McElreath, 2020), denoting the range of probable values in which the true value could fall (Kruschke, 2014); and 2) we computed the probability of direction (hereafter: *pd*; Makowski et al., 2019). The 89 % CrI reveals the range within which an effect falls with 89 % probability (McElreath, 2020), while the *pd* indicates the probability that a parameter is strictly positive or negative (Makowski et al., 2019). For all models, diagnostics revealed an accurate reflection of the original response values by the posterior distributions, as R-hat statistics were < 1.01, the numbers of effective samples >1000, and MCMC chains had no divergent transitions (see ESM, Figure S1; Bürkner, 2017). Furthermore, diagnostics also revealed an accurate reflection of the original response values by the posterior distributions (see ESM, Figure S2).

2.4.2. Event-level analyses: Testing species differences

We fitted two Bayesian Generalised Linear Mixed Models (GLMMs) to investigate whether consolation was more likely to occur in bonobos or chimpanzees. The sample for this model consisted of $N = 276$ events (PC $N = 214$; PD $N = 62$) of $N = 90$ apes (bonobo $N = 40$; chimpanzee $N = 50$). The first model (hereafter: *Model 1.1*) fitted a Bernoulli distribution (consolation occurrence: 1 = yes; 0 = no) and the second model (hereafter: *Model 1.2*) fitted a Poisson distribution (count of consolations per event). The fixed effects structure for these models included species and the number of bystanders. As population sizes varied across the three groups, and consolation may be more likely if there are more individuals present, we included the number of bystanders as a control effect to improve the accuracy of the estimated fixed effect of species. The random effects structure consisted of random intercepts for aggressor identity and victim identity, as well as random slopes for number of bystanders within both aggressor identity and victim identity.

2.4.3. *Dyad-level analyses: Testing individual and social factors*

To test how individual and social factors influenced consolatory tendencies, we fitted two GLMMs to our dyad-level data for each species separately (Baayen et al., 2008). Each observation row represented a particular bystander-victim combination present during a given victim follow event. Two bonobos and three chimpanzees were excluded due to long periods of absence from their main groups (bonobos: 62–95 % of observation time; chimpanzees: 54–65 % of observation time). The sample for the bonobo model (hereafter: *Model 2.1*) consisted of $N = 1656$ observation rows from $N = 38$ individuals observed across $N = 116$ events within $N = 2$ groups. The sample for the chimpanzee model (hereafter: *Model 2.2*) consisted of $N = 5668$ observation rows from $N = 47$ individuals observed across $N = 160$ within $N = 1$ group.

Our response variable constituted a binary outcome fitted with a Bernoulli distribution according to whether the bystander solicited affiliative contact to the victim focal during the 5-min event (consolation occurrence: 1 = yes; 0 = no). Full models included individual factors of the bystander (age, rank, sex), the victim (age, rank, and sex), and the social relationship of the dyad (kinship) as fixed effects. Unfortunately, due to inconsistencies in the social affiliation data collection protocol between Lola ya Bonobo and Chimfunshi, we were unable to include quantitative measures for gregariousness and dyadic affiliation score in the bonobo model. The chimpanzee model did however include fixed effects for bystander gregariousness and dyadic affiliation score. For both species, we also included the interaction of bystander age and bystander sex as a fixed effect and the bonobo model additionally included group as a fixed effect. The random effects structure for each model consisted of random intercepts for the individual identities of the aggressor, bystander, and victim as random effects as well as the event ID. We also included theoretically identifiable random slopes of victim age and sex within bystander identity and bystander age and sex within victim identity.

3. Results

3.1. *Event-level results: Do bonobos console more than chimpanzees?*

Across observations, consolation occurred at least once in 127 of the 276 events (46.0 %). On average, $M = 0.64$ ($SD = 0.81$) consolatory approaches occurred per event in bonobos, and $M = 0.75$ ($SD = 1.00$) consolatory approaches per event in chimpanzees.[1] *Model 1.1* revealed no effect of species on the probability of consolation occurring at least once in an event ($b = 0.08$, $SD = 0.33$, 89 % credible interval (CrI) $[-0.94, 1.11]$, *pd*: 0.55; see Fig. 1). Additionally, *Model 1.2* showed no effect of species on the count of consolers that responded per event ($b = 0.08$, $SD = 0.33$, 89 % CrI $[-0.44, 0.60]$, $pd = 0.60$). Importantly, in each model, the inclusion of the number of bystanders also did not influence the outcome variables (*Model 1.1*: $b = 0.13$, $SD = 0.15$, 89 % CrI $[-0.36, 0.62]$, $pd = 0.66$; *Model 1.2*: $b = 0.13$, $SD = 0.15$, 89 % CrI $[-0.12, 0.37]$, $pd = 0.80$), indicating consolation likelihood does not increase if more possible consolers are present. Output from the event-level models can be seen in Table S3 (ESM).

3.2. *Dyad-level results: Which within-species factors drive consolation tendencies?*

A full table of the output for bonobos (*Model 2.1*) and chimpanzees (*Model 2.2*) can be seen in Table S4 (ESM).

3.2.1. *Social effects*

We found a very strong effect of kin dyads consoling more than non-kin dyads in bonobos ($b = -2.35$, $SD = 0.62$, 89 % CI $[-3.37, -1.37]$), $pd = 1.00$; Fig. 2), but not in chimpanzees ($b = -0.46$, $SD = 0.46$, 89 % CrI $[-1.17, 0.29]$, $pd = 0.84$; Fig. 2). We also found a very strong positive effect of affiliation level on consolation in chimpanzees ($b = 0.26$, $SD = 0.10$, 89 % CrI $[0.11, 0.42]$, $pd = 1.00$; see Fig. 2). Furthermore, in chimpanzees, we found no clear effect of bystander gregariousness (chimpanzees: $b = -0.17$, $SD = 0.21$, 89 % CrI $[-0.51, 0.16]$, $pd = 0.80$). Finally, for bonobos we found no clear evidence for an effect of group ($b = -0.49$, $SD = 0.52$, 89 % CrI $[-1.34, 0.32]$, $pd = 0.83$).

3.2.2. *Victim characteristics*

In bonobos, we found a very strong negative effect of victim age where younger bonobos were consoled more than older bonobos ($b = -1.59$, $SD = 0.74$, 89 % CrI $[-2.88, -0.55]$, $pd = 1.00$; see Fig. 3), but no credible effect in chimpanzees ($b = 0.29$, $SD = 0.25$, 89 % CrI $[-0.11, 0.68]$, $pd = 0.88$; see Fig. 3). We found no credible effects for victim sex in either species (bonobos: $b = 1.08$, $SD = 0.97$, 89 % CrI $[-0.36, 2.68]$, $pd = 0.88$; chimpanzees: $b = -0.51$, $SD = 0.64$, 89 % CrI $[-1.56, 0.45]$, $pd = 0.79$). Victim rank had no credible effect on consolation tendency in either bonobos or chimpanzees (see ESM, Table S4).

3.2.3. *Bystander characteristics*

We found no clear effect of an interaction between bystander age and bystander sex in bonobos ($b = -0.81$, $SD = 0.89$, 89 % CrI $[-2.32, 0.50]$, $pd = 0.67$), however, there was evidence of a strong positive effect of bystander age ($b = -0.74$, $SD =$, 89 % CrI $[-1.64, 0.12]$, $pd = 1.00$; see Fig. 4) indicating that younger bystanders may console more than older bystanders. However, for chimpanzees we found moderate evidence for an interaction between bystander age and bystander sex ($b = -0.78$, $SD = 0.62$, 89 % CrI $[-1.76, 0.19]$, $pd = 0.90$; see Fig. 4). This interaction indicates that indicated that younger individuals of both species consoled more than older individuals, with young males consoling more than females. However, males appear to decrease in their consolation tendency at a steeper rate than females. Conditional probability plots of these interactions are shown in Figure S3 (ESM). Bystander rank had no credible effect on consolation tendency in chimpanzees (see ESM, Table S4). However, high-ranking bonobos consoled victims more than low-ranking bonobos (low vs. high: $b = -1.01$, $SD = 0.50$, 89 % CrI $[-1.81, -0.24]$, $pd = 0.98$) but there was no credible difference between medium- and high-ranking bystanders (medium vs. high: $b = -0.43$, $SD = 0.51$, 89 % CrI $[-1.44, 0.57]$, $pd = 0.81$).

4. Discussion

Systematic cross-species comparisons are vital for elucidating the evolutionary origins for complex socio-emotional behaviours, including empathy. Human research has revealed substantial individual and cultural variation in emotional responding and this study indicates that this may be the case for our closest living relatives. Our results indicate that bonobos and chimpanzees do not significantly differ in their tendency to engage in consolation—considered a behavioural expression of empathy—both in terms of the behaviour's overall occurrence and the number of consolers that respond per event. Furthermore, these findings reflect recent others that contrast with previously held assumed species dichotomisations, such as in aggression (Mouginot et al., 2024), social tolerance (van Leeuwen et al., 2023), and the use of sexual behaviour during social tension (Brooker et al., 2025). We did, however, find several within-species trends in potential drivers of consolatory tendencies. Expressions of empathy and other emotion-related behaviour are known to vary in wild chimpanzee communities of the same subspecies (Arnold & Whiten, 2001; Kutsukake & Castles, 2004), which parallels findings across diverse human cultures (Chopik et al., 2017). The presence of considerable intraspecies variation in these sanctuary great apes complements this literature and suggests that empathic

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[1] To account for potential false positives in our consolation analyses, we estimated the proportion of post-conflict affiliations that may have occurred by chance using previously reported dispersed PC–MC rates (Fraser et al., 2008; Clay & de Waal, 2013). Based on these estimates, we conservatively approximate that ~12 % (9/72) of chimpanzee events featuring 1+ consolation and ~20.2 % (11/55) of bonobo events featuring consolation may be false positives.

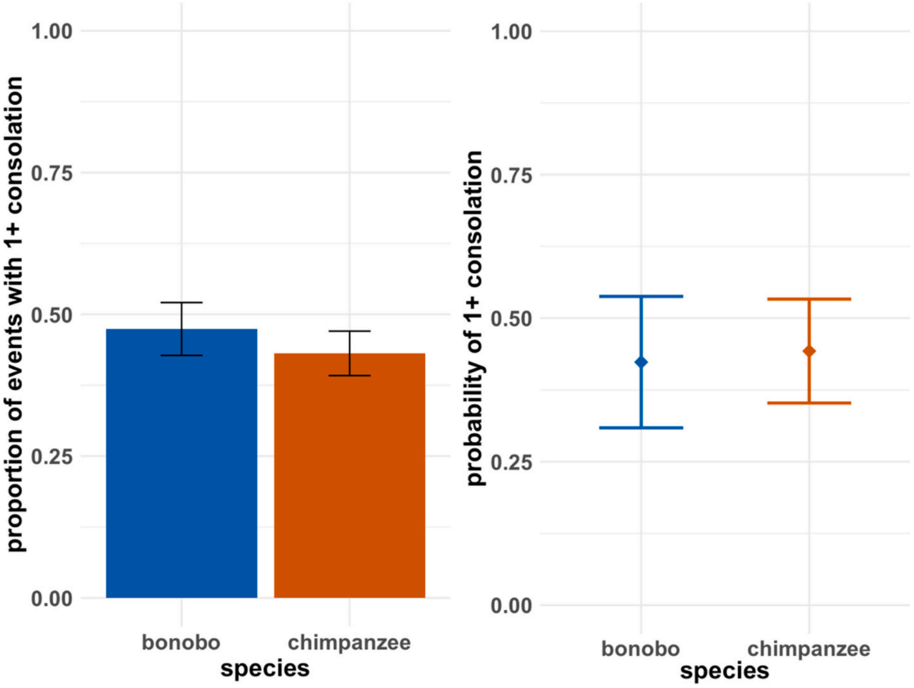

Fig. 1. Barplot (left) and conditional probability plot (right) showing no credible difference between bonobos and chimpanzees in their relative tendency for a PC or PD event to feature 1+ consolation approach towards a distressed victim. Results obtained from *Model 1.1*. Whiskers on barplot show one standard error above and below mean. Probability plot shows conditional effect of species with 89 % credible intervals.

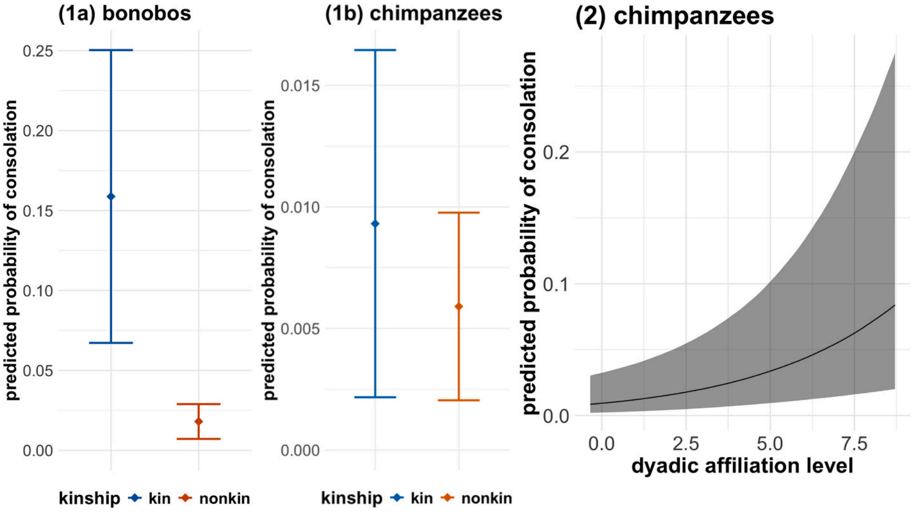

Fig. 2. Predicted probability plots showing credible effect of kinship in bonobos (1a) and chimpanzees (1b) and a credible effect of dyadic affiliation level in chimpanzees (2). For all plots, Y-axis = predicted probability of consolation. (1a-1b) X-axis = kinship. Square points and error bars correspond to posterior means and the upper and lower 89 % credible intervals, respectively. (2) X-axis = z-transformed dyadic affiliation level. Shaded area corresponds to 89 % credibility intervals. Dyadic affiliation level not tested in bonobos.

tendencies may be shaped by broader individual and social circumstances.

Our findings complement previous consolation research in *Pan* by showing that bystander age is an important predictor of consolation in bonobo and chimpanzee communities (Clay & de Waal, 2013a; Webb et al., 2017). Although underlying mechanisms cannot be detected in an observational study, it is possible that young individuals may console more than older individuals as they are typically afforded more social tolerance before they become fully embedded into their respective group's dominance dynamics (de Waal, 1986). Furthermore, younger individuals may be less inhibitive with their responses in these contexts. We did not measure individual's capacity for inhibition in this study. However, an interesting follow-up would be to compare these two species on inhibition, such as through delayed gratification tasks (Beran et al., 1999), and investigate if this measure predicts an individual's relative tendency to console.

Consistent with the theory that social closeness predicts empathic responses (Anderson & Keltner, 2002; Preston & de Waal, 2002), we found that kin partners were more likely to console one another in bonobos. In chimpanzees, we were able to test dyadic affiliation levels, finding that consolation was biased towards closer social partners generally. Previous investigations on these bonobo groups revealed

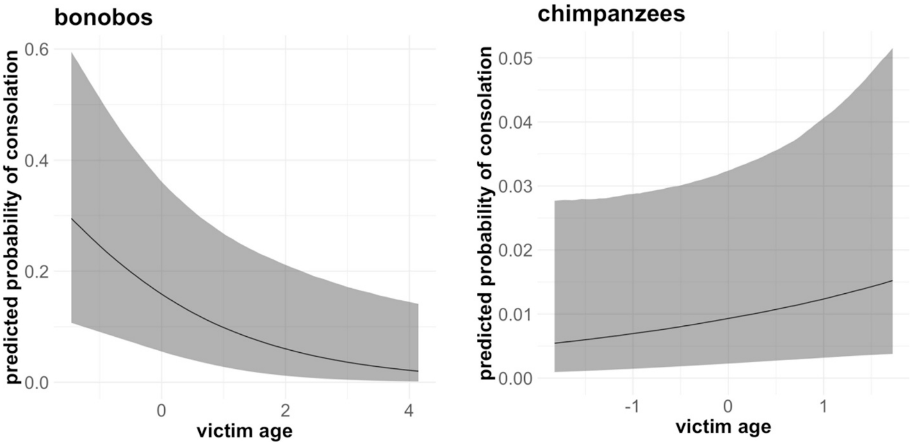

Fig. 3. Predicted probability plot showing credible main effect of victim age in bonobos (left) and no credible effect in chimpanzees (right). X-axis = z-transformed age. Y-axis = predicted probability of consolation. Shaded area corresponds to 89 % credibility intervals.

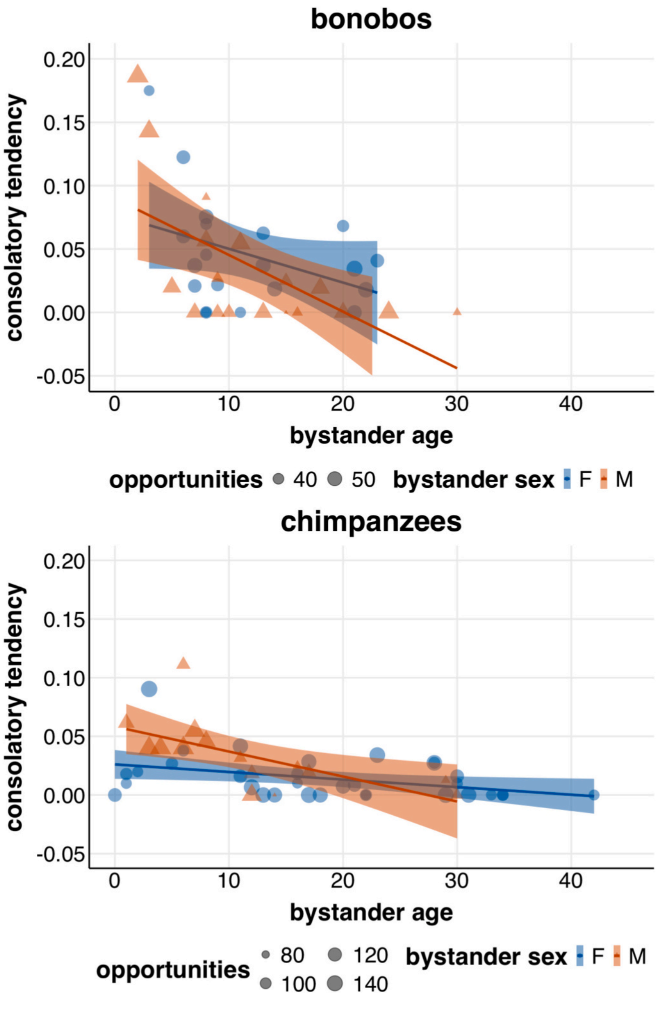

Fig. 4. Scatterplot showing credible main effect of bystander age in bonobos (top) and moderate evidence for an interaction between bystander age and sex in chimpanzees (bottom). X-axis = age in years. Y-axis = consolation/total opportunities to console. Females = blue circles; males = red triangles. Point size reflects number of events the individual was present as a bystander. Note, this plot provides a simple visualisation of the aggregated raw data using frequentist 95 % confidence limits for ease of comparison. See Figure S3 (ESM) for predicted probability plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

strong influences of social relationship on consolation occurrences (Clay & de Waal, 2013a). These findings further emphasize the role of relational proximity in facilitating empathy, suggesting that both species exhibit a preference for consoling individuals with whom they share close, reciprocal ties. Temporal variation in consolatory efforts may reflect empathy as a phenomenon that emerges flexibly when social conditions permit (Brooker et al., 2022). Understanding the nuances of such affiliative behaviour may elucidate the adaptive value of empathy in primate social networks.

It is possible that consolation may serve different functions in bonobo and chimpanzee societies. Chimpanzees may be more selective in their responses as wild and captive communities have been well-documented to exhibit political social lives, centred around strong adult male-male alliances and displays of dominance and subordinacy (Gruber & Clay, 2016). This may be further evidenced by a possible age-sex interaction in chimpanzees, whereby young males were the most consolatory and older individuals were the least consolatory. Enhanced responsiveness in young male chimpanzees may represent a drive to form and reinforce strong social bonds with their close peers and older individuals they will spend their lives with (Mitani, 2009). Furthermore, adult male chimpanzees were much less likely to be followed as distressed focals ($N = 17/160$) compared to adult females ($N = 103/160$). Therefore, opportunities for adult male chimpanzees to console their closest social partners were respectively low and may additionally explain the direction of the age-sex interaction whereby older males were as unlikely to console as adult females. In the Kanyawara community at Kibale Chimpanzee Project in Uganda, young male chimpanzees are typically more likely to be victims of aggression, which may be due to their tendencies to elicit the most aggression themselves (Sabbi et al., 2021). Regardless, social bonds formed during male chimpanzee development predict dominance trajectories (Bray & Gilby, 2020). Thus, this effect at a young age in chimpanzees may be caused by younger males watching their peers being aggressed often during a period when they are building foundational relationships for later life (Sandel et al., 2020).

In contrast, in bonobos, males typically only form strong relationships with their mothers (Surbeck et al., 2011) and occasionally other females for mating and alliance formation (Surbeck et al., 2012). Despite males being the philopatric sex for both species, only chimpanzee communities tend to feature strong male-male relationships (Gruber & Clay, 2016). Furthermore, the political dynamics in bonobo societies appear to be relatively more subtle, and thus difficult to study (Furuichi, 2011). Instead, bonobos may be less selective and respond out of care and socio-emotional sensitivity towards others (Clay & de Waal, 2013b; F. Kano et al., 2015; Kret et al., 2016). Bonobos tended to console victims of both sexes and all ranks evenly. Furthermore, in line with recent findings that paedomorphic signalling increases likelihood of receiving consolation (Heesen et al., 2022), younger bonobo victims were generally more likely to be consoled. However, higher-ranked bonobo bystanders did offer consolation more than those of low rank, indicating that lower social standing may inhibit individuals to approach distressed peers. A deeper, longitudinal comparison with more groups of each species is needed to reveal the extent to which consolation has a political association across age, rank, and sex combinations in each species. Furthermore, a more specialist analysis testing whether lower stakes and reduced severity in juvenile aggression—for example following play escalation and outside of the political landscape—leads to more flexible consolation responses supporting the initial development of long-term social bonds.

In this study, we imposed strict criteria of inclusion for consolation, where any behaviour following a solicitation from the victim was not counted. For example, if a victim immediately approached a bystander and solicited an interaction with them, any subsequent interactions initiated by the bystander during the PC/PD period were not coded as consolatory approaches. As consolation is linked with empathy, if bystanders are not the party to solicit contact then it is not possible to infer that they may have been motivated by the victim's distress to respond (de Waal & Aureli, 1996; de Waal & Preston, 2017). Therefore, there is also a possibility that victim-initiated interactions provided reassurance and comfort to the victim, yet these encounters were not counted in our analyses. A wider investigation into bystander-victim interactions following distress could reveal whether the intraspecies trends found in this study are associated with empathic tendencies, or wider conflict management responses in general (Clay et al., 2016).

Intraspecies variation is vital for comparative research across taxa (Kaufhold & van Leeuwen, 2019), especially for studying behaviour where responses are influenced by social structures and dynamic relationships. As such, studies of primates have revealed substantial intergroup behavioural variation. Examples include bartering in long-tailed macaques (*Macaca fascicularis*; Brotcorne et al., 2017), activity and ranging in guerezas (*Colobus guereza*; Fashing, 2001), and even the connectedness of social networks in vervets (*Chlorocebus pygerythrus*; Borgeaud et al., 2016). The *Pan* apes similarly can vary between groups regarding expressions of various social and ecological behaviours. Examples include, but are by no means limited to, grooming traditions (van Leeuwen et al., 2012) and communication in chimpanzees (Crockford et al., 2004), and hunting behaviour and tool use in bonobos (Hohmann & Fruth, 2003).

Another characteristic that varies within the *Pan* apes is social tolerance (Cronin et al., 2014; Cronin et al., 2015; van Leeuwen et al., 2023), a factor posited to facilitate empathy according to the *Social Constraints Hypothesis* (de Waal & Aureli, 1996; Palagi et al., 2014). The *Social Constraints Hypothesis* has been suggested to explain why some primates express empathic behaviour and others do not (de Waal & Aureli, 1996; Palagi et al., 2014). Despite the longstanding notion that bonobos are more socially tolerant than chimpanzees (Hare et al., 2007, 2012), recent studies suggest that variation in social tolerance is more pronounced at the group level within each species (Mouginot et al., 2024; van Leeuwen et al., 2023), challenging the idea that such differences might underlie species-specific patterns of empathy.

Furthermore, apparent neurobiological predispositions for enhanced socio-emotional responsiveness in bonobos (Rilling et al., 2012; Staes et al., 2014) does not determine greater empathic potential over chimpanzees. Consolation proclivity in bonobos and chimpanzees may depend more on community dynamics, such as the presence of kin relationships and juveniles. It is not possible to extrapolate group differences with only two communities, however, when controlling for all other factors, we found no credible difference between bonobo groups in consolation tendency. Future research should assess tolerance levels and risk of aggression of multiple groups and compare these alongside demographic factors with relative tendencies to console to elucidate any group-level variation in consolation across the *Pan* apes.

5. Conclusion

In sum, our findings support the notion that within-species community variation among *Pan* behavioural tendencies may be more significant than between-species differences (Gruber & Clay, 2016; Kaufhold & van Leeuwen, 2019; McGrew et al., 2001). Both bonobos and chimpanzees are highly flexible and adaptable species, and under particular conditions and pressures may exhibit greater or reduced tendencies to express empathy-related behaviours like consolation. In humans, we see individual- and group-level variation in behaviours such as communication, prosociality, conformity, and empathy and other socio-emotional responses that may be facilitated by certain social dynamics and cultural norms (Chopik et al., 2017; House et al., 2013; Hua et al., 2019; van Leeuwen et al., 2018). The same may be true in our closest living relatives. Further research into species comparisons should always integrate group-level differences (e.g., composition, collective temperaments) that may promote or hinder empathic expressions such as consolation. Comparing more groups of the same species and investigating within-group drivers of various empathy-related behaviours may reveal a deep ancestral history of such cultural flexibility in emotional responsiveness, and what features promote or hinder the expression of empathy.

Author's note and dedication

Prior to his passing, Prof. Frans de Waal reviewed and contributed to the original submission of this manuscript, and he remains a co-author. In recognition of his pioneering research, unwavering support, and mentorship, we dedicate this paper to Prof. de Waal's memory and enduring legacy.

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CRediT authorship contribution statement

Jake S. Brooker: Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Christine E. Webb:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **Stephanie Kordon:** Investigation, Writing – original draft. **Frans B.M. de Waal:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft. **Zanna Clay:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare no potential competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2025.106682.

Data availability

The data associated with this research are available at OSF: https://osf.io/hqtek/, doi: 10.17605/OSF.IO/4CXV9.

References

Adriaense, J. E. C., Koski, S. E., Huber, L., & Lamm, C. (2020). Challenges in the comparative study of empathy and related phenomena in animals. *Neuroscience & Biobehavioral Reviews, 112*, 62–82. https://doi.org/10.1016/j.neubiorev.2020.01.021

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3–4), 227–266. https://doi.org/10.1163/156853974X00534

Anderson, C., & Keltner, D. (2002). The role of empathy in the formation and maintenance of social bonds. *Behavioral and Brain Sciences, 25*(1), 21–22. https://doi.org/10.1017/S0140525X02230010

Arnold, K., & Whiten, A. (2001). Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour, 138*, 649–690. https://doi.org/10.1163/156853901316924520

Baayen, R. H., Davidson, R. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language, 59*(4), 390–412. https://doi.org/10.1016/j.jml.2007.12.005

Batson, C. D., Fultz, J., & Schoenrade, P. A. (1987). Distress and empathy: Two qualitatively distinct vicarious emotions with different motivational consequences. *Journal of Personality, 55*(1), 19–39. https://doi.org/10.1111/j.1467-6494.1987.tb00426.x

Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L., & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 34*(2), 119–127. https://doi.org/10.1002/(SICI)1098-2302(199903)34:2<119::AID-DEV5>3.0.CO;2-P

Borgeaud, C., Sosa, S., Bshary, R., Sueur, C., & van de Waal, E. (2016). Intergroup variation of social relationships in wild Vervet monkeys: A dynamic network approach. *Frontiers in Psychology, 7*. https://doi.org/10.3389/fpsyg.2016.00915

Bray, J., & Gilby, I. C. (2020). Social relationships among adult male chimpanzees (*Pan troglodytes schweinfurthii*): Variation in the strength and quality of social bonds. *Behavioral Ecology and Sociobiology, 74*(9), 112. https://doi.org/10.1007/s00265-020-02892-3

Brooker, J. S., Webb, C. E., & Clay, Z. (2022). Primate empathy: A flexible and multi-componential phenomenon. In B. L. Schwartz, & M. J. Beran (Eds.), *Primate Cognitive Studies* (pp. 505–532). Cambridge University Press. https://doi.org/10.31234/osf.io/bpw5x.

Brooker, J. S., Webb, C. E., de Waal, F. B. M., & Clay, Z. (2024). The expression of empathy in human's closest relatives, bonobos and chimpanzees: Current and future directions. *Biological Reviews, 99*(4), 1556–1575. https://doi.org/10.1111/brv.13080

Brooker, J. S., Webb, C. E., van Leeuwen, Kordon, S., de Waal, … Clay, Z. (2025). Bonobos and chimpanzees overlap in sexual behaviour patterns during periods of social tension. *Royal Society Open Science, 12*, 242031. https://doi.org/10.1098/rsos.242031

Brotcorne, F., Giraud, G., Gunst, N., Fuentes, A., Wandia, I. N., Beudels-Jamar, R. C., … Leca, J.-B. (2017). Intergroup variation in robbing and bartering by long-tailed macaques at Uluwatu Temple (Bali, Indonesia). *Primates, 58*(4), 505–516. https://doi.org/10.1007/s10329-017-0611-1

Burkett, J. P., Andari, E., Johnson, Z. V., Curry, D. C., de Waal, F. B. M., & Young, L. J. (2016). Oxytocin-dependent consolation behavior in rodents. *Science, 351*(6271), 375–378. https://doi.org/10.1126/science.aac4785

Bürkner, P.-C. (2017). Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software, 80*, 1–28. https://doi.org/10.18637/jss.v080.i01

Chopik, W. J., O'Brien, E., & Konrath, S. H. (2017). Differences in empathic concern and perspective taking across 63 countries. *Journal of Cross-Cultural Psychology, 48*(1), 23–38. https://doi.org/10.1177/0022022116673910

Clay, Z., & de Waal, F. B. M. (2013a). Bonobos respond to distress in others: Consolation across the age spectrum. *PLoS One, 8*(1), Article e55206. https://doi.org/10.1371/journal.pone.0055206

Clay, Z., & de Waal, F. B. M. (2013b). Development of socio-emotional competence in bonobos. *Proceedings of the National Academy of Sciences, 110*(45), 18121. https://doi.org/10.1073/pnas.1316449110

Clay, Z., Furuichi, T., & de Waal, F. B. M. (2016). Obstacles and catalysts to peaceful coexistence in chimpanzees and bonobos. *Behaviour, 153*(9–11), 1293–1330. https://doi.org/10.1163/1568539X-00003335

Crockford, C., Herbinger, I., Vigilant, L., & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology, 110*(3), 221–243. https://doi.org/10.1111/j.1439-0310.2004.00968.x

Cronin, K. A., De Groot, E., & Stevens, J. M. G. (2015). Bonobos show limited social tolerance in a group setting: A comparison with chimpanzees and a test of the relational model. *Folia Primatologica, 86*(3), 164–177. https://doi.org/10.1159/000373886

Cronin, K. A., van Leeuwen, E. J. C., Vreeman, V., & Haun, D. B. M. (2014). Population-level variability in the social climates of four chimpanzee societies. *Evolution and Human Behavior, 35*(5), 389–396. https://doi.org/10.1016/j.evolhumbehav.2014.05.004

Das, M., Penke, Z., & van Hooff, J. A. R. A. M. (1998). Postconflict affiliation and stress-related behavior of long-tailed macaque aggressors. *International Journal of Primatology, 19*(1), 53–71. https://doi.org/10.1023/A:1020354826422

Davidov, M., Paz, Y., Roth-Hanania, R., Uzefovsky, F., Orlitsky, T., Mankuta, D., & Zahn-Waxler, C. (2021). Caring babies: Concern for others in distress during infancy. *Developmental Science, 24*(2), Article e13016. https://doi.org/10.1111/desc.13016

Decety, J., & Lamm, C. (2006). Human empathy through the Lens of social neuroscience. *The Scientific World Journal, 6*, 1146–1163. https://doi.org/10.1100/tsw.2006.221

Decety, J., Norman, G. J., Berntson, G. G., & Cacioppo, J. T. (2012). A neurobehavioral evolutionary perspective on the mechanisms underlying empathy. *Progress in Neurobiology, 98*(1), 38–48. https://doi.org/10.1016/j.pneurobio.2012.05.001

Eisenberg, N., Carlo, G., Murphy, B., & van Court, P. (1995). Prosocial development in late adolescence: A longitudinal study. *Child Development, 66*(4), 1179–1197. https://doi.org/10.1111/j.1467-8624.1995.tb00930.x

Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Maszk, P., Smith, M., … Suh, K. (1994). The relations of emotionality and regulation to dispositional and situational empathy-related responding. *Journal of Personality and Social Psychology, 66*(4), 776–797. https://doi.org/10.1037/0022-3514.66.4.776

Eisenberg, N., Guthrie, I. K., Murphy, B. C., Shepard, S. A., Cumberland, A., & Carlo, G. (1999). Consistency and development of prosocial dispositions: A longitudinal study. *Child Development, 70*(6), 1360–1372. https://doi.org/10.1111/1467-8624.00100

Eisenberg, N., & Strayer, J. (1990). *Empathy and its development*. CUP Archive.

ELAN (Version 5.8). (2019). Computer software. In *Max planck institute for psycholinguistics, the language archive*. https://archive.mpi.nl/tla/elan.

Fashing, P. J. (2001). Activity and ranging patterns of Guerezas in the Kakamega Forest: Intergroup variation and implications for intragroup feeding competition. *International Journal of Primatology, 22*(4), 549–577. https://doi.org/10.1023/A:1010785517852

Fraser, O. N., & Bugnyar, T. (2010). Do ravens show consolation? Responses to Distressed Others. *PLoS One, 5*(5), Article e10605. https://doi.org/10.1371/journal.pone.0010605

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences, 105*(25), 8557–8562. https://doi.org/10.1073/pnas.0804141105

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology: Issues, News, and Reviews, 20*(4), 131–142. https://doi.org/10.1002/evan.20308

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Belknap Press of Harvard University Press. https://repository.library.georgetown.edu/handle/10822/811357.

Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology: Issues, News, and Reviews, 25*(5), 239–252. https://doi.org/10.1002/evan.21501

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*(7), 619–623. https://doi.org/10.1016/j.cub.2007.02.040

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*(3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007

Heesen, R., Austry, D. A., Upton, Z., & Clay, Z. (2022). Flexible signalling strategies by victims mediate post-conflict interactions in bonobos. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 377*(1860), Article 20210310. https://doi.org/10.1098/rstb.2021.0310

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS One, 5*(8), Article e12438. https://doi.org/10.1371/journal.pone.0012438

Hohmann, G., & Fruth, B. (2003). Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology, 44*(4), 563–571. https://doi.org/10.1086/377649

House, B. R., Silk, J. B., Henrich, J., Barrett, H. C., Scelza, B. A., Boyette, A. H., … Laurence, S. (2013). Ontogeny of prosocial behavior across diverse societies. *Proceedings of the National Academy of Sciences, 110*(36), 14586–14591. https://doi.org/10.1073/pnas.1221217110

Hua, X., Greenhill, S. J., Cardillo, M., Schneemann, H., & Bromham, L. (2019). The ecological drivers of variation in global language diversity. *Nature. Communications, 10*(1). https://doi.org/10.1038/s41467-019-09842-2. Article 1.

Kaburu, S. S. K., & Newton-Fisher, N. E. (2015). Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behaviour, 99*, 61–71. https://doi.org/10.1016/j.anbehav.2014.10.018

Kano, F., Hirata, S., & Call, J. (2015). Social attention in the two species of Pan: Bonobos make more eye contact than chimpanzees. *PLoS One, 10*(6), Article e0129684. https://doi.org/10.1371/journal.pone.0129684

Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford University Press.

Kaufhold, S. P., & van Leeuwen, E. J. C. (2019). Why intergroup variation matters for understanding behaviour. *Biology Letters, 15*(11), Article 20190695. https://doi.org/10.1098/rsbl.2019.0695

Knafo, A., Zahn-Waxler, C., Van Hulle, C., Robinson, J. L., & Rhee, S. H. (2008). The developmental origins of a disposition toward empathy: Genetic and environmental contributions. *Emotion, 8*, 737–752. https://doi.org/10.1037/a0014179

Kret, M. E., Jaasma, L., Bionda, T., & Wijnen, J. G. (2016). Bonobos (Pan paniscus) show an attentional bias toward conspecifics' emotions. *Proceedings of the National*

Academy of Sciences of the United States of America, 113(14), 3761–3766. https://doi.org/10.1073/pnas.1522060113

Kruschke, J. (2014). *Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan.* Academic Press.

Kutsukake, N., & Castles, D. L. (2004). Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates, 45*(3), 157–165. https://doi.org/10.1007/s10329-004-0082-z

van Leeuwen, E. J. C., Cohen, E., Collier-Baker, E., Rapold, C. J., Schäfer, M., Schütte, S., & Haun, D. B. M. (2018). The development of human social learning across seven societies. *Nature Communications, 9*(1). https://doi.org/10.1038/s41467-018-04468-2. Article 1.

van Leeuwen, E. J. C., Cronin, K. A., Haun, D. B. M., Mundry, R., & Bodamer, M. D. (2012). Neighbouring chimpanzee communities show different preferences in social grooming behaviour. *Proceedings of the Royal Society B: Biological Sciences, 279*(1746), 4362–4367. https://doi.org/10.1098/rspb.2012.1543

van Leeuwen, E. J. C., Staes, N., Brooker, J. S., Kordon, S., Nolte, S., Clay, Z., … Stevens, J. M. G. (2023). Group-specific expressions of co-feeding tolerance in bonobos and chimpanzees preclude dichotomous species generalizations. *iScience, 26*(12), Article 108528. https://doi.org/10.1016/j.isci.2023.108528

Lindegaard, M. R., Liebst, L. S., Bernasco, W., Heinskou, M. B., Philpot, R., Levine, M., & Verbeek, P. (2017). Consolation in the aftermath of robberies resembles post-aggression consolation in chimpanzees. *PLoS One, 12*(5). https://doi.org/10.1371/journal.pone.0177725

Lockwood, P. L., Seara-Cardoso, A., & Viding, E. (2014). Emotion regulation moderates the association between empathy and prosocial behavior. *PLoS One, 9*(5), Article e96555. https://doi.org/10.1371/journal.pone.0096555

Lucchesi, S., Cheng, L., Deschner, T., Mundry, R., Wessling, E. G., & Surbeck, M. (2020). Better together? How intergroup associations affect energy balance and feeding behavior in wild bonobos. *Behavioral Ecology and Sociobiology, 75*(1), 2. https://doi.org/10.1007/s00265-020-02943-9

Makowski, D., Ben-Shachar, M. S., Chen, S. H. A., & Lüdecke, D. (2019). Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology, 10*. https://doi.org/10.3389/fpsyg.2019.02767

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and STAN* (2nd ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9780429029608

McGrew, W. C., Marchant, L. F., Scott, S. E., & Tutin, C. E. G. (2001). Intergroup differences in a social custom of wild chimpanzees: The grooming hand-clasp of the Mahale Mountains. *Current Anthropology, 42*(1), 148–153. https://doi.org/10.1086/318441

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour, 77*(3), 633–640. https://doi.org/10.1016/j.anbehav.2008.11.021

Mouginot, M., Wilson, M. L., Desai, N., & Surbeck, M. (2024). Differences in expression of male aggression between wild bonobos and chimpanzees. *Current Biology, 34*(8), 1780–1785.e4. https://doi.org/10.1016/j.cub.2024.02.071

Neumann, C., & Kulik, L. (2020). EloRating: Animal dominance hierarchies by Elo rating (Version 0.46.11) [computer software]. https://CRAN.R-project.org/package=EloRating.

Nishida, T., Zamma, K., Matsusaka, T., Inaba, A., & McGrew, W. C. (2010). *Chimpanzee behavior in the wild: An audio-visual encyclopedia.* Springer Science & Business Media.

Norscia, I., & Palagi, E. (2011). Yawn contagion and empathy in *Homo sapiens*. *PLoS One, 6*(12), Article e28472. https://doi.org/10.1371/journal.pone.0028472

Palagi, E., Dall'Olio, S., Demuru, E., & Stanyon, R. (2014). Exploring the evolutionary foundations of empathy: Consolation in monkeys. *Evolution and Human Behavior, 35*(4), 341–349. https://doi.org/10.1016/j.evolhumbehav.2014.04.002

Palagi, E., & Norscia, I. (2013). Bonobos protect and console friends and kin. *PLoS One, 8*(11), Article e79290. https://doi.org/10.1371/journal.pone.0079290

Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology, 62*(1), 15–30. https://doi.org/10.1002/ajp.20000

Pérez-Manrique, A., & Gomila, A. (2018). The comparative study of empathy: Sympathetic concern and empathic perspective-taking in non-human animals. *Biological Reviews, 93*(1), 248–269. https://doi.org/10.1111/brv.12342

Plotnik, J. M., & de Waal, F. B. M. (2014). Asian elephants (*Elephas maximus*) reassure others in distress. *PeerJ, 2*, Article e278. https://doi.org/10.7717/peerj.278

Pollerhoff, L., Stietz, J., Depow, G. J., Inzlicht, M., Kanske, P., Li, S.-C., & Reiter, A. M. F. (2022). Investigating adult age differences in real-life empathy, prosociality, and well-being using experience sampling. *Scientific Reports, 12*, 3450. https://doi.org/10.1038/s41598-022-06620-x

Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences, 25*(1), 1–20. https://doi.org/10.1017/S0140525X02000018

Rilling, J. K., Scholz, J., Preuss, T. M., Glasser, M. F., Errangi, B. K., & Behrens, T. E. (2012). Differences between chimpanzees and bonobos in neural systems supporting social cognition. *Social Cognitive and Affective Neuroscience, 7*(4), 369–379. https://doi.org/10.1093/scan/nsr017

Romero, T., Castellanos, M. A., & de Waal, F. B. M. (2010). Consolation as possible expression of sympathetic concern among chimpanzees. *Proceedings of the National Academy of Sciences, 107*(27), 12110–12115. https://doi.org/10.1073/pnas.1006991107

RStudio Team. (2020). RStudio: Integrated development for R (Version 1.3.1093) [computer software]. http://www.rstudio.com/.

Sabbi, K. H., Emery Thompson, M., Machanda, Z. P., Otali, E., Wrangham, R. W., & Muller, M. N. (2021). Sex differences in early experience and the development of aggression in wild chimpanzees. *Proceedings of the National Academy of Sciences, 118*(12), Article e2017144118. https://doi.org/10.1073/pnas.2017144118

Sandel, A. A., Langergraber, K. E., & Mitani, J. C. (2020). Adolescent male chimpanzees (*Pan troglodytes*) form social bonds with their brothers and others during the transition to adulthood. *American Journal of Primatology, 82*(1), Article e23091. https://doi.org/10.1002/ajp.23091

Staes, N., Stevens, J. M. G., Helsen, P., Hillyer, M., Korody, M., & Eens, M. (2014). Oxytocin and vasopressin receptor gene variation as a Proximate Base for inter- and intraspecific behavioral differences in bonobos and chimpanzees. *PLoS One, 9*(11), Article e113364. https://doi.org/10.1371/journal.pone.0113364

Stimpson, C. D., Barger, N., Taglialatela, J. P., Gendron-Fitzpatrick, A., Hof, P. R., Hopkins, W. D., & Sherwood, C. C. (2016). Differential serotonergic innervation of the amygdala in bonobos and chimpanzees. *Social Cognitive and Affective Neuroscience, 11*(3), 413–422. https://doi.org/10.1093/scan/nsv128

Surbeck, M., Deschner, T., Schubert, G., Weltring, A., & Hohmann, G. (2012). Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Animal Behaviour, 83*(3), 659–669. https://doi.org/10.1016/j.anbehav.2011.12.010

Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., … Mundry, R. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. *Royal Society Open Science, 4*(5), Article 161081. https://doi.org/10.1098/rsos.161081

Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B: Biological Sciences, 278*(1705), 590–598. https://doi.org/10.1098/rspb.2010.1572

Tokuyama, N., Emikey, B., Bafike, B., Isolumbo, B., Iyokango, B., Mulavwa, M. N., & Furuichi, T. (2012). Bonobos apparently search for a lost member injured by a snare. Primates. *Journal of Primatology, 53*(3), 215–219. https://doi.org/10.1007/s10329-012-0298-2

de Waal, F. B. M. (1986). The integration of dominance and social bonding in Primates. *The Quarterly Review of Biology, 61*(4), 459–479. https://doi.org/10.1086/415144

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour, 106*(3–4), 183–251. https://doi.org/10.1163/156853988X00269

de Waal, F. B. M. (2007). The 'Russian doll' model of empathy and imitation. In S. Bråten (Ed.), *On being moved: From mirror neurons to empathy* (pp. 49–69). John Benjamins Publishing Company. https://doi.org/10.1075/aicr.68.06waa.

de Waal, F. B. M. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology, 59*(1), 279–300. https://doi.org/10.1146/annurev.psych.59.103006.093625

de Waal, F. B. M., & Aureli, F. (1996). Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 80–110). Cambridge University Press. https://books.google.com/books/about/Reaching_Into_Thought.html?id=rqcQcQoYAFoC.

de Waal, F. B. M., & Preston, S. D. (2017). Mammalian empathy: Behavioural manifestations and neural basis. *Nature Reviews Neuroscience, 18*(8). https://doi.org/10.1038/nrn.2017.72. Article 8.

de Waal, F. B. M., & Yoshihara, D. (1983). Reconciliation and redirected affection in Rhesus monkeys. *Behaviour, 85*(3–4), 224–241. https://doi.org/10.1163/156853983X00237

Wark, J. D., Cronin, K. A., Niemann, T., Shender, M. A., Horrigan, A., Kao, A., & Ross, M. R. (2019). Monitoring the behavior and habitat use of animals to enhance welfare using the ZooMonitor app. *Animal Behavior and Cognition, 6*(3), 158–167. https://doi.org/10.26451/abc.06.03.01.2019

Webb, C. E., Romero, T., Franks, B., & de Waal, F. B. M. (2017). Long-term consistency in chimpanzee consolation behaviour reflects empathetic personalities. *Nature Communications, 8*, 1–8. https://doi.org/10.1038/s41467-017-00360-7. London.

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., … Wrangham, R. W. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature, 513*(7518), 414–417. https://doi.org/10.1038/nature13727

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology, 32*(1), 363–392. https://doi.org/10.1146/annurev.anthro.32.061002.120046

Wittenburg, P., Brugman, H., Russel, A., Klassmann, A., & Sloetjes, H. (2006). *ELAN: A professional framework for multimodality research* (pp. 1556–1559). https://pure.mpg.de/pubman/faces/ViewItemOverviewPage.jsp?itemId=item_60436.

Wittig, R., & Boesch, C. (2003). The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour, 140*(11–12), 1527–1559. https://doi.org/10.1163/156853903771980701